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Errata: In my earlier paper the references to Williams's papers should have been cited as Trans. Ent. Soc. Lond. not Trans. Zool. Soc. Lond.

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SOME FIELD OBSERVATIONS ON THE BACHACS OF TRINIDAD

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INTRODUCTION

Since 1969, the Overseas Development Administration of the British Government has financed research on leaf-cutting ants (bachacs) with the aim of devising efficient control methods for those species which are considered pests. Several scientists in Britain are involved with the project and at least one person is based in South America to carry out most of the field work. Up until very recently, the field work on this project has been done in Trinidad and this together with the laboratory studies done in the U.K., means that much of our understanding of these insects is based on those species occuring on this island.

Before attempting to control a pest in the field, one must be thoroughly familar with its biology, including its ecology, behaviour and so on. The leaf-cutting ant project is no exception. Over the past five years we have accumulated a great deal of knowledge as regards the biology of these ants and the purpose of this article is to summarise for the general naturalist some of the information that has emerged out of this and other people's work.

It would be impossible to cover all aspects of the biology of these interesting insects in a short article. In view of this, more attention has been paid to those behavioural aspects which the field naturalist may observe himself.

THE SPECIES IN TRINIDAD

There are only two species of bachac in Trinidad although several other ants are incorrectly given this name. Most people do not distinguish between these two species but to the entomologist and the serious naturalist the two are very different in both structure and habits. These differences warrant the placing of these ants in two separate genera. **Atta cephalotes (L)** (Fig. 1a-f) or the forest bachac as it is sometimes called, has a shiny appearance, is reddish-brown in colour and has long slender legs. This species is not confined to Trinidad for its distribution extends from Central America to Brazil. The majority of the nests are to be found in natural or semi-natural rain forest. **Acromyrmex octospinosus** (Reich.) (Fig. 1g-l) is a more ubiquitous species. The workers are generally smaller than those of **Atta** and there is no soldier caste. These ants vary in colour from brown to almost black and the legs are short compared with those of the previous species. It nests in various habitats including walls, under stones, under fallen tree trunks and in the ground itself.

LIFE CYCLE

Bachacs, like many other ants, have regular flights of winged males and females (Fig. 1) from the parent colonies. In Trinidad, **Atta cephalotes** and **Acromyrmex octospinosus** fly at about the same time with the former species reaching peak activity in July or August and the latter in May or June. The winged males and females of **Atta** (Fig. 1. d, e, f) are large, conspicuous insects about one inch (2.54 cm) in length. Those of **Acromyrmex** are smaller by comparison (Fig. 1. j, k, l) measuring about half an inch (1.27 cm) in total length. In both types the sexes can be told apart by the size of the head. In the males the width of the head capsule at its hind margin is never greater than half the width of the thorax, whereas in the females the head is as wide as or slightly less wide than the thorax.

A single female may copulate with several males either from a single nest or from different nests. In this was she builds up a store of sperm that will have to last her up to 20 years. Having mated, the young queen breaks off her wings by pushing them with her legs and proceeds to dig into the soil. She excavates a vertical tunnel and when this is a few inches deep (about 1 foot in **Atta**.) she proceeds to enlarge it to form a small chamber slightly to one side of the main shaft (Fig. 2). When the excavation of the nest is complete the queen spits out a small wad of

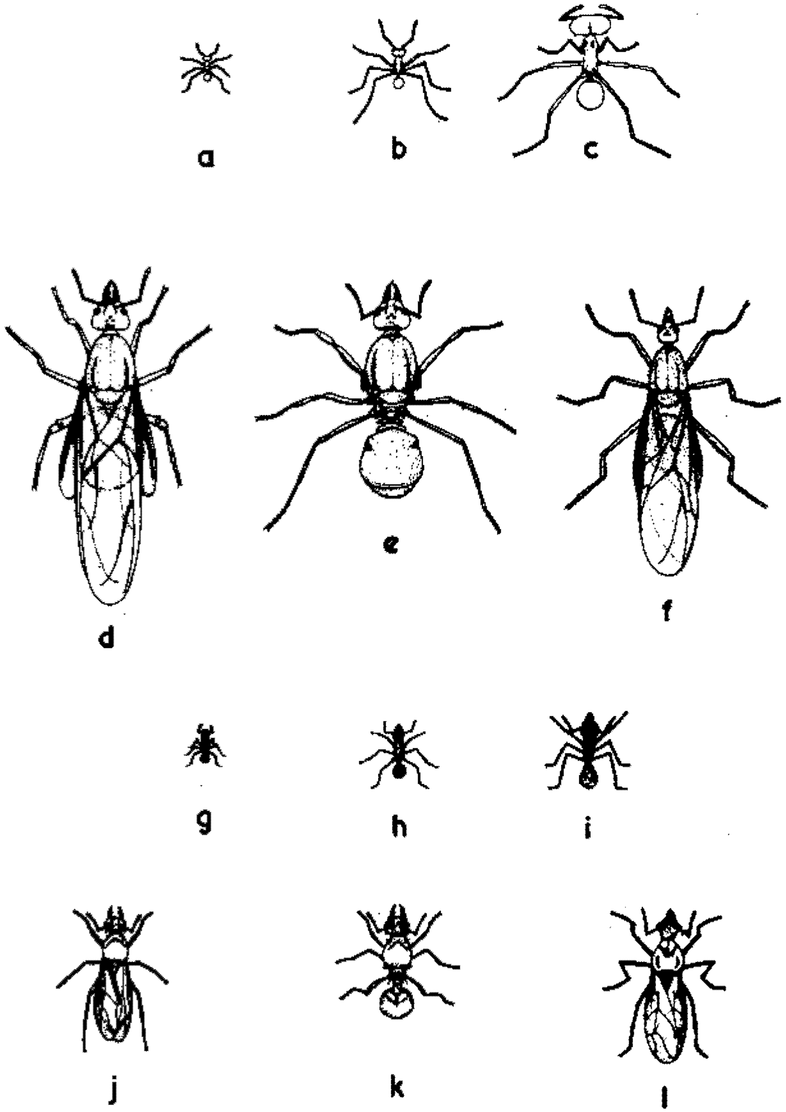


Fig 1. Various castes of Atta cephalotes and **Acromyrmex octospinosus.**
Atta a–f. Acromyrmex g–l.
(a) small worker (minim); (b) medium sized worker; (c) soldier **(maxim); (d)** winged queen; (e) wingless queen; **(f)** winged **male; (g)** small worker; (h) medium-sized worker; (i) large worker; (j) winged queen; (k) wingless queen; (l) winged male.

fungus from her mouth. This fungus she has collected before leaving the parental nest. As the fungus grows, the young queen periodically leaves the nest and searches for fresh leaves in the immediate vicinity. These cut leaves are then taken back into the nest and are chewed into a sticky green pulp which is added as substrate for the developing fungus. In **Atta cephalotes** at least, the first viable eggs hatch to give small workers (Fig. 1. a) in about 70 days. These ants leave the nest on short distance foraging excursions, returning with leaf fragments for the rapidly expanding fungus gardens.

DEVELOPMENT OF THE NEST

As the colony ages, so the number of ants and the size of the nest increases. The workers excavate more chambers to accommodate further fungus gardens. Even after 2 or 3 years, a colony of **Atta cephalotes** is made up of many hundreds of thousands of individuals. Some records suggest that a 6-year old nest could contain anything up to 5 million individuals. Colonies of **Acromyrmex** never reach this size and a nest of 100,000 individuals would be considered a large one. The smaller size of **Acromyrmex** nests is probably one reason why the species is to be found nesting in many different types of habitat.

Whilst the colony is expending obvious changes are taking place in the general appearance of the nest. In **Atta cephalotes** for example, when the new queen first excavates the primary chamber she forms a small crater with the discarded soil (Fig. 2). The crater then becomes a turret or chimney by the activity of the first brood of workers about 70 days later (Fig. 3). The nest remains in this condition for the first year of its life and thereafter reverts again to a crater shape of increasing size. As the nest expends more and more craters appear on the surface. A colony of **Atta cephalotes** probably starts producing winged sexual forms after 2 or 3 years and therefore can be considered mature at this stage, although over the next few years the nest will increase greatly in size.

A mature nest will contain many fungus gardens, varying from the size of a tennis ball to that of a football. Normally the fungus gardens are concealed in subterranean chambers and can only be examined when the nest is excavated. When the fungus garden is examined it is seen to be made up of minutely subdivided pieces of leaf, often withered to a brown colour, and covered with fine strands of a delicate white fungus. At certain points the fungus appears in the form of compact clusters, the 'staphylae', which the ants pick and feed to their larvae.

There is also a substantial turn-over of material in these gardens. As the fungus develops so it depletes the macerated leaves of their nutrients and eventually there is so little fungal growth that the whole garden is broken up and discarded in the deeper parts of the nest.

Another conspicuous activity of the mature nest is that of soil disposal by the workers. As the nest grows, more and more chambers have to be excavated to accommodate the increasing number of fungus gardens. The soil from these areas is carried out onto the surface of the nest and dumped in a selected spot.

FORAGING BEHAVIOUR

As the nest increases in size, foraging becomes more organised. Foraging behaviour reaches its peak of development in the genus **Atta** presumably in response to the large complex social system operating here. **Atta cephalotes** for example builds well defined trails about six inches wide and often over 100 yards long. Although a large nest of **Acromyrmex octospinosus** has long trails leading from it, they are never as conspicuous as those produced by **Atta.**

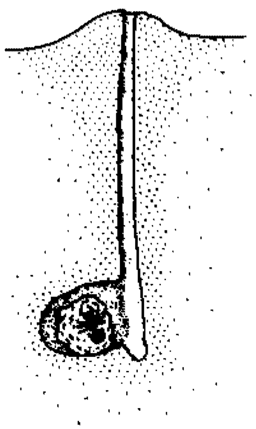
Recent work carried out in Trinidad (Lewis et al, 1974b) has shown that both **Atta** and **Acromyrmex** have well defined foraging cycles. Using automatic ant counters, Lewis and his colleagues were able to record continuously over a period of several months, the numbers of ants leaving the nest on foraging missions at different times of the day. They found that **Atta cephalotes** is a predominately nocturnal forager. Foraging commences regularly at about 19.00 hours, reaches a peak of activity at about 21.00 hours and then subsides by about 06.00 hours. However, not all the foraging follows this pattern. Less frequently the ants of some nests forage during the day. Again the regularity of the rhythm is striking. The workers in such a nest would start foraging in earnest about 09.30 hours, build up to a maximum about 13.00 hours and foraging would cease by 19.00 hours.

Different foraging trails leading into the same nest would sometimes be out of phase, that is to say that whilst the ants on one trail were nocturnal, the ants on the other trail were diurnal. The situation is further complicated by the fact that on certain occasions the ants on a particular trail would change from being nocturnal to being diurnal or vice versa. This change over in 'shift work' does not occur suddenly but the regular rhythmicity falters for about two days before the new rhyhtm is established. The reasons for these peculiar but interesting cycles of behaviour are not at all clear. Lewis et al., (1974a) have examined a variety of environmental factors such as temperature, light intensity and rainfall in an attempt to correlate these with foraging patterns but no obvious correlations emerged from these investigations. They have suggested that it may be the nutritional requirements of the brood and/or fungus gardens which determine whether foraging occurs at night or during the day, since it is well established that the nutrient content of leaves alters at different times of the 24-hour day.

In tropical rain forest with its abundance of plant species, **Atta cephalotes** will cut the leaves of many different plants. For example, Cherrett (1968) working in Guyana for a 10-week period recorded a single colony as having cut at least 36 different types of plant in this time. Among this range of species, some were obviously preferred to others, and some species also present in the forest were not attacked at all. That bachacs attack different plants is not unusual in that many species of insects and other animals are polyphagous or 'general herbivores'. What is strange and something appreciated by the astute naturalist is the spatial distribution of bachac foraging. Examination of an **Atta** nest in the forest, and the vegetation in an area 50 yards radius from it, will soon reveal that the ants travel far to cut particular trees when there are specimens of the same species closer to the nest. What then are the reasons for this behaviour? Attempting to explain the situation, Cherrett (1968) has put forward the following plausible theory. He believes that the foraging system used by **Atta** is efficient in conserving the natural balance of plant species in the forest. If a large **Atta** colony attacked all the suitable specimens nearest it, then this sort of grazing pressure would certainly kill many of them off. These cleared areas would probably then be invaded by species resistant to leaf-cutting ant attack. There is no evidence to suggest in fact that the plants nearer to the nest are any more resistant than the ones further away.

The process of leaf cutting is interesting and the field naturalist would be well advised to spend some time studying it. The first thing to notice is that young foliage is attacked in preference to old. Physical factors are partly responsible for this, older leaves becoming tougher and therefore more resistant. Barrer and Cherrett (1972) have also shown that chemical factors are also important in determining which leaves on a particular plant will be attacked. It seems that young leaves possess attractive chemicals which induce cutting, but when the leaf gets older there is a build-up of repellent chemicals which tend to counteract other leaf cutting stimuli.

Another feature worth noting is that of the pattern of cutting on individual leaves. Examination of Figure 4 shows that the cuts are not evenly distributed but that once a cut has been made it acts as a focus for further cutting. Barrer and Cherrett (1972) examined this phenomenon in some detail and were able to show that a cut edge has both physical and chemical properties that make it more likely to be cut than an intact leaf edge.



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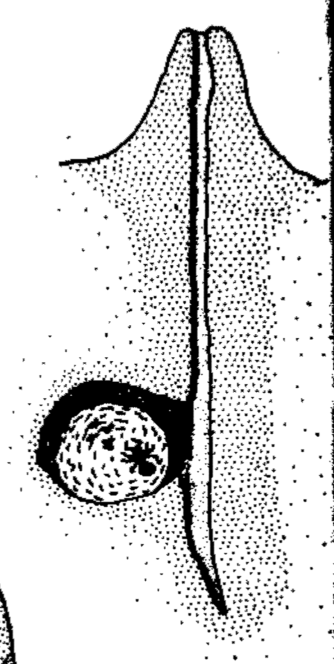

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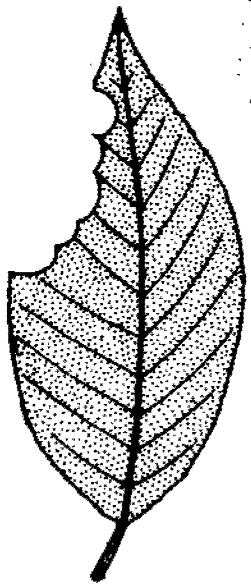

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Fig. 2. Young nest of **Atta cephalotes** at the small crater stage.

Fig. 3 Slightly older nest of **Atta cephalotes** at the chimney stage.

Fig 4. Typical **Atta cephalotes** damage to a leaf.

During leaf cutting the mandibles of the worker ant are used in very much the same way as one uses a tin opener. One mandible is inserted onto the leaf tissue and does not contribute much to the actual cutting whilst the other mandible is pulled through the leaf. Having completed the cut, the ant manipulates the leaf segment into a position ready for carrying. Because the fragment weighs as much as or even more than the ant itself, getting it into the correct position is important. The leaf is normally carried with its centre of gravity directly above the ant.

Close examination of a column of **Atta** foragers will reveal the presence of small worker ants (minima) on many of the leaf fragments being carried back to the nest. Usually there is only one minim per leaf section but there can be more. What then is the function of these 'hitchhikers'? Weber (1972) proposes that they serve a dual function. In the first place they lick the surface of the leaf and it has been suggested that they are removing debris and alien organisms. The fungus cultured by the ants is a pure culture and therefore it is important that foreign fungi are excluded. Another function of the 'hitchhiker' is that they fend off parasitic phorid flies. Some of these flies are known to lay eggs on the adult ant in which they develop as internal parasites. When these phorids are about, the minima workers rear up on their middle and hind legs and fend off the flies with their fore legs, antennae and mandibles.

OTHER ANIMALS ASSOCIATED WITH THE ANTS

A variety of animals is associated with the bachacs either as guests, parasites or predators. Mites, springtails (Collembola), nematode worms and phorid flies are to be found in the nests, whilst some amphibians and mammals are predators. The common giant toad (**Bufo marinus**) in Trinidad feeds on bachacs as well as on many other ant species. Also the silky anteater (**Tamandua longicauda**) takes both the species of bachac in its specialised diet. Another interesting animal, the legless lizard (**Amphisbaena**) is also quite commonly found in nests of both **Atta** and **Acromyrmex** in Trinidad.

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BREEDING SEASON AND BREEDING SIZE OF FEMALE *EMERITA PORTORICENSIS* SCHMITT (CRUSTACEA: ANOMURA) IN TRINIDAD, WEST INDIES

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Emerita portoricensis Schmitt is common on several of the beaches of Trinidad (Fig. 1). It is the small burrowing crustacean that Trinidadians know as sea armadillo, sea tatoo or sea cockroach, but which elsewhere is called mole crab or sand crab. However, since chitons, which are molluscs, are also called sea cockroach, any of the other common names is preferable to this. Chitons are sessile but **Emerita** is relatively active, moving with the tides so that it occupies the zone where the waves flow on to the beach. It spends most of its time buried in the wet sand but in feeding extends a pair of antennae above the sand as a wave begins to recede and traps on their feathery structure the microscopic particles in the water that form its diet.

Female **Emerita** carry their eggs on bristle-like abdominal appendages (pleopods) and since the eggs are usually bright orange they are easy to see, especially if the telson or last abdominal segment is pulled back from its normal position under the rest of the adbomen. It was the ease of observation of egg-bearing that suggested to me this study which had at first the simple objective of determining the breeding season. Later, a second objective was added as described below.

My methods were simple. I visited Maracas Bay every two or three weeks with the intention of catching and examining twenty adults. However, on many occasions the animals were difficult to find and I had to be satisfied with fewer. I simply walked extremely slowly along the beach looking for the animals' extended antennae and dug up those judged to be adult from the size of the antennae. Each individual was then examined for eggs and replaced. By moving in one direction the chance of catching the same individual more than once was minimized. These methods would not be used by a professional zoologist but they gave a clear-cut answer to any query nonetheless: **Emerita** breeds all the year round. The detailed results are shown in Table 1 where it can be seen that there was no occasion on which the beach was visited without finding ovigerous females.

TABLE I

The numbers of ovigerous females of **E. portoricensis** at Maracas Bay, 1971–1972.

Date	No. in Sample	No. Ovig.	% Ovig.
2 May '71	10	6	60
16 May '71	2	2	100
30 May '71	20	12	60
20 Jun '71	9	5	55
4 Jul '71	1	1	100
26 Sep '71	20	12	60
17 Oct '71	20	14	70
7 Nov '71	16	8	50
14 Nov '71	10	9	90
5 Dec '71	15	12	80
26 Dec '71	5	3	60
9 Jan '72	6	4	66
30 Jan '72	10	5	50
20 Feb '72	10	9	90
12 Mar '72	7	4	56
7 Apr '72	20	14	70
2 May '72	1	1	100
9 Jul '72	20	16	80
30 Jul '72	10	6	60
20 Aug '72	10	10	100
3 Sep '72	10	4	40

During the course of the study it became obvious that ovigerous females usually made up much more than half the number of individuals examined and that their size varied considerably. However, if each sample were made up of males and females of which only